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Influence of Inbreeding and Other Factors on Litter Size in Chester White Swine

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PURPOSE AND PLAN OF EXPERIMENT

It is generally recognized that litter size in swine is subject to a considerable amount of variation, but little is known about the influence of genetic and environmental factors on this character. From a practical standpoint, it is highly desirable that there be a better understanding of the part played by each of these groups of causes, for such information is essential in establishing the effectiveness of any breeding program designed to increase litter size.

The experiment on which this study is based was initiated by the Bureau of Animal Industry in the spring of 1922.[1] The primary object was to develop, by a system of close inbreeding, strains of Chester White, Tamworth, and Poland China to be used in various genetic and nongenetic experiments. Another object was to cross some of the inbred strains for the purpose of evaluating the merits of pigs produced by such a procedure.

The original plan of the experiment was to use matings between only full brothers and sisters. This system of breeding was closely adhered to in the Poland Chinas and Tamworths, and only a few matings in these breeds were made between individuals less closely related than full sibs. Breeding plans involving the Chester Whites, though also calling for the use of matings between only full brothers and sisters, were subsequently changed to include matings other than those of sibs. Some of the general results obtained during the course of the experiment have been published in annual reports of the

[1] The experiment was directed until 1927 by Sewall Wright, formerly of the Bureau; from 1927 to 1935 inclusive by Hugh C. McPhee; and since 1935 by J. H. Zeller.

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Bureau, and a more detailed report of the results with the Poland Chinas has been made by McPhee, Russell, and Zeller (*9*).[2]

The purpose of this paper is to present an analysis of the results obtained with the Chester White breed. Discussion is directed primarily to the effects of inbreeding and other factors on litter size at birth, at 28 days, and at 70 days of age.

MATERIAL AND METHODS

The Chester Whites used as foundation stock consisted of 2 boars and 5 sows. Four of the sows had produced litters as early as 1921, but not until 1924 were any of their progeny used for breeding purposes. Besides the foundation animals, 13 boars and 5 sows were subsequently brought into the herd. All additional breeding animals, 40 boars and 108 sows, were descendants of the foundation animals and of those purchased later. Neither the foundation animals nor those purchased later were inbred within 2 generations back of their sires and dams, and the degree of relationship between any of them and their mates did not exceed 4 percent. Inbreeding and relationship coefficients were calculated according to the method of Wright (*12*).

According to the pedigree records, no planned inbreeding was practiced until 1925, when the first full brother-sister matings were made. Some of the pigs raised that year were mated to their full sibs, whereas others were used in matings between less closely related animals as well as in distinct outcrosses. This plan was followed throughout the major part of the experiment. However, because of the scarcity of progeny produced by certain matings in some years, the proportions of litters produced by the various types of matings were not the same in all years. In one case an inbred line was successfully maintained for seven generations of full brother-sister matings.

Selection of animals for breeding was based primarily on conformation and vigor, but consideration also was given to size of litter and rate of growth. The management was comparable to that of a well-kept commercial herd, and every effort was made to keep environmental conditions as uniform as possible. All sows were fed good standard rations, and each sow was placed in a separate pen prior to farrowing. The sows generally were bred to farrow both spring and fall litters. All pigs were allowed free range on pasture lots, usually from the first week after birth until weaning, which was at 70 days of age.

The data were analyzed mainly by the method of analysis of variance described by Fisher (*2*) and Snedecor (*10*). By this method, the data are classified according to certain criteria which it is thought are significant causes of variation, and the variance is analyzed into its component parts. The relation between the total variance and that left after subtracting the variance between classes may be expressed either as a correlation between members of the same class or as that portion of the total variance which disappears after allowing for the effect of that factor or group of factors which are common to all members of a class. The method for testing significance was the F test of Snedecor (*10*).

[2] Italic numbers in parentheses refer to Literature Cited, p. 10.

EXPERIMENTAL RESULTS

Changes in Degree of Inbreeding

The average inbreeding of the boars and sows used as parents each year from 1921 to 1937, inclusive, together with that of their litters, is shown in figure 1. The average inbreeding of the 55 boars used as sires during the course of the experiment was 29.2 percent; of the 118 sows used as dams, 20.5 percent; and of the 362 litters farrowed, 20.1 percent. Approximately 34 percent of the boars, 50 percent of the sows, and 48 percent of the litters were less than 5-percent inbred.

As shown in figure 1, the average inbreeding of the litters and that of their parents were similar in most years. There was no tendency,

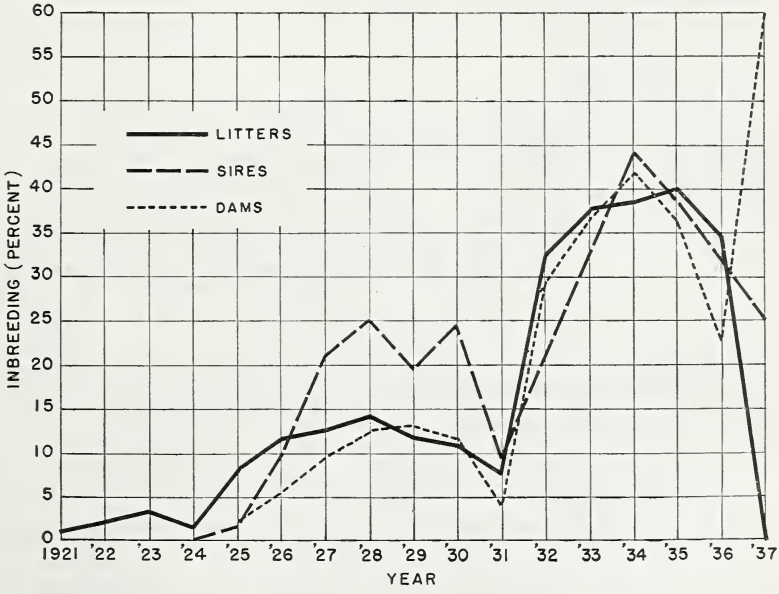

FIGURE 1.—Average percentage of inbreeding of the boars and sows used as parents each year from 1921 to 1937, inclusive, together with that of their litters.

however, for the inbreeding of the herd to increase at a uniform rate. This result is due to the varying proportions of litters produced by the different kinds of matings in different years.

Changes in Number of Pigs Per Litter

The average numbers of pigs per litter at birth, at 28 days, and at 70 days of age are given by years in figure 2. The mean sizes of all litters included in the study were 8.7 pigs per litter at birth, 6.2 at 28 days, and 5.8 at 70 days.

There are rather marked fluctuations in the average numbers of pigs per litter from one year to another. There is, however, a fairly high degree of parallelism between those fluctuations. It may be

concluded, therefore, that except for a few years, the proportions of pigs raised from birth to 28 days and to 70 days were much the same in most years.

Of greater interest than these results, however, is the distinct downward trend in litter size exhibited by each age group. This trend, when considered in conjunction with the yearly fluctuations, was highly significant in all cases.

Effects of Inbreeding

The curves in figure 2 illustrate not only that litter size is a highly variable character but also that it may show a marked decline during a relatively small number of years. Because of the considerable

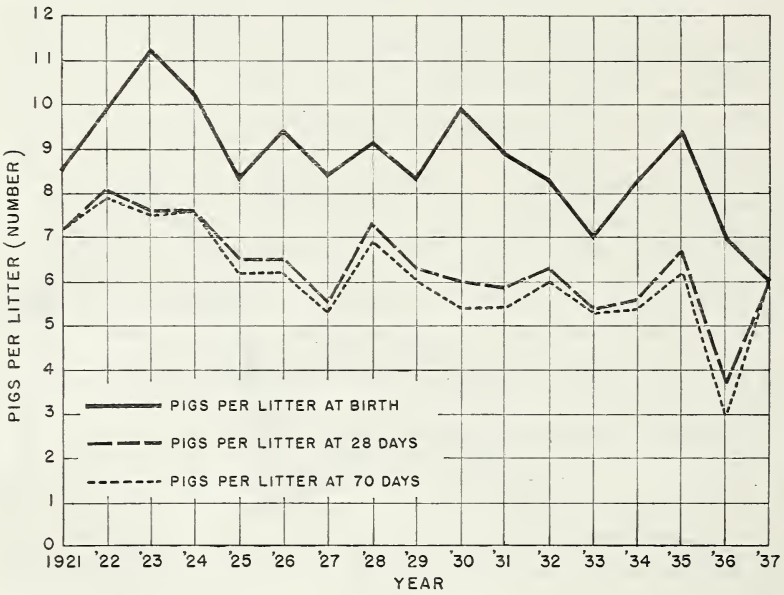

Figure 2.—Average numbers of pigs per litter at birth, at 28 days, and at 70 days of age in each year from 1921 to 1937, inclusive.

amount of inbreeding practiced in the experiment, it is reasonable to believe that the decline was at least partly due to inbreeding. To determine what effect inbreeding had on litter size, the regression of litter size on the inbreeding of the litters and that of their sires and dams was calculated by use of an analysis of multiple covariance on an intrayear basis.

Table 1 shows the standard regression coefficients for litter size at birth, at 28 days, and at 70 days of age on the inbreeding of the dams, sires, and litters. Accepting the within-year coefficients as the best estimates available for evaluating the effects of inbreeding, one sees that litter size was not significantly affected by differences in the inbreeding of the sires and dams. The regression coefficients of litter size on the inbreeding of the litters, on the other hand, indicate that there was a tendency for the more highly inbred litters to be significantly smaller at each of the three ages than were outbred or

less highly inbred litters. Based on these results, the conclusion seems justified that inbreeding was, as suspected, at least partly responsible for the gradual decline in litter size.

TABLE 1.—*Total and intrayear regressions of litter size (X) on inbreeding of dams (A), sires (B), and litters (C)*

Item	Regression coefficients for litter size at—								
	Birth			28 days			70 days		
	β_{XA}	β_{XB}	β_{XC}	β_{XA}	β_{XB}	β_{XC}	β_{XA}	β_{XB}	β_{XC}
Total	−0.145	+0.127	[1] −0.293	+0.020	+0.080	[1] −0.313	+0.078	+0.091	[2] −0.372
Within years	−.129	+.098	[1] −.253	+.003	+.116	[1] −.278	+.026	+.148	[2] −.327

[1] Significant (P=0.01 to 0.05).
[2] Highly significant (P=<0.01).

Insofar as litter size is a product of the reproductive capacity of the sire and dam, on the one hand, and of the viability of the pigs, on the other, the results likewise suggest that it was primarily the latter which was adversely affected by inbreeding. Thus although inbreeding had no apparent effect on the reproductive capacity of either the boars or the sows, it evidently was too intense to prevent the fixation of genes deleterious to the viability of the pigs.

INFLUENCE OF YEAR

Since the litters used in this study were farrowed during a period of 17 years, it was thought desirable to determine the extent to which litter size was affected by yearly variations in environmental conditions. Unfortunately no method was found to arrive at an indisputable answer to this question, for changes in the genetic level [3] of the herd for litter size undoubtedly account for a part of the year-to-year variations in the number of pigs per litter. However, if the reasonable assumption is made that changes in the genetic level of the herd not resulting from inbreeding, were of minor importance, it is possible to obtain a fair estimate of the relative importance of environmental factors not uniform from one year to another. This was accomplished by use of an analysis of multiple covariance according to the year in which the litters were farrowed.

A comparison of the fifth and ninth columns of table 2 shows no material difference in the results obtained for litter size at 28 days and at 70 days of age. The variance between years, when compared with the variance between litters farrowed in the same year, was significant or highly significant both before and after allowance was made for the effects of inbreeding.

As regards litter size at birth, on the other hand, it was only before allowance was made for the effects of inbreeding that yearly differences were statistically significant. The results lead to the deduction, therefore, that in the case of litter size at 28 days and at 70 days, factors associated with feeding and management had a real effect, whereas in litter size at birth, most if not all of the yearly variations

[3] Genetic level signifies average performance of the herd so far as it is determined by genetic factors.

were due to the fixation by inbreeding of genes unfavorable to the production of large litters. Correction for the effects of inbreeding reveals that approximately 3.7 and 5.5 percent, respectively, of the variance in litter size at 28 days and at 70 days disappears when only pigs farrowed in the same year are considered. This is only a small fraction of the total variance and probably is too small to be of much practical importance.

TABLE 2.—*Analysis of multiple covariance between litter size as the dependent variable and the inbreeding of the sires, dams, and litters as independent variables*

Age of pigs (days)	Source of variance	Degrees of freedom	Litter size		R^2	Errors of estimate		
			Sum of squares	Mean square		Degrees of freedom	Sum of squares	Mean square
0	Between years	16	315	[1] 19.7		16	230	14.4
	Within years	345	3,255	9.436	[1] 0.079	342	2,998	8.767
	Total	361	3,570	9.890	[1] .096	358	3,228	9.016
28	Between years	16	258	[1] 16.1		16	202	[2] 12.6
	Within years	345	2,403	6.966	[1] .033	342	2,323	6.795
	Total	361	2,661	7.372	[1] .051	358	2,525	7.055
70	Between years	16	305	[1] 19.0		16	250	[1] 15.6
	Within years	345	2,407	6.976	[1] .037	342	2,317	6.777
	Total	361	2,712	7.512	[1] .053	358	2,567	7.172

[1] Highly significant (P=<0.01).
[2] Significant (P=0.01 to 0.05).

Influence of Season

Table 3 shows the average numbers of pigs per litter at birth, at 28 days, and at 70 days of age according to the season of farrow. Spring farrowing was mostly in March, April, and May, although a few sows had litters as early as February or as late as June. Most of the fall litters were farrowed in September and October with a few litters in August and November.

TABLE 3.—*Average size of litter at birth, at 28 days, and at 70 days of age, classed by season of birth*

Season	Litters	Average number of pigs per litter at—		
		Birth	28 days	70 days
	Number	*Number*	*Number*	*Number*
Spring	225	8.8	6.4	6.1
Fall	137	8.4	5.8	5.4
Total	362	8.7	6.2	5.8

Spring-farrowed litters were somewhat larger than fall-farrowed litters, but only in number of pigs at 70 days of age was the seasonal effect statistically significant. However, less than 1 percent of the variance in number of pigs at this age was found to be due to season of birth.

Influence of Age of Dam

Table 4 shows the number and average size of litters at birth, at 28 days, and at 70 days of age, grouped according to age of dams at farrowing. There was a fairly consistent tendency for litter size to increase with increasing age of dams to about 42 months, after which it remained nearly constant to 66 months. A similar though slightly more curvilinear relationship for number of pigs per litter at birth was found by Ellinger (*1*), Johansson (*4*), Keith (*5*), Krallinger and Gruhn (*6*), Križenecký (*7*), and others.

Table 4.—*Average size of litter at birth, at 28 days, and at 70 days of age, classified by age of dam at farrowing*

Age of dam (months)	Litters	Average number of pigs per litter at—			Age of dam (months)	Litters	Average number of pigs per litter at—		
		Birth	28 days	70 days			Birth	28 days	70 days
	Number	*Number*	*Number*	*Number*		*Number*	*Number*	*Number*	*Number*
12	77	7.2	4.9	4.5	48	22	10.0	6.0	5.9
18	47	7.4	5.8	5.6	54	10	9.9	6.7	6.4
24	61	8.6	6.6	6.1	60	10	10.3	6.1	5.8
30	55	9.1	6.8	6.5	66	5	10.4	7.2	7.2
36	44	9.7	6.7	6.5	72	3	7.3	4.7	4.3
42	28	10.3	6.8	6.6	Total	362	8.7	6.2	5.8

An analysis of variance made on the basis of age of dam shows that the age effect was highly significant for litter size at birth, at 28 days, and at 70 days of age. In number of pigs per litter at birth, approximately 10.7 percent of the variance was eliminated by taking out the differences between age means. The portion of the variance thus accounted for among the litters at 28 and at 70 days of age was 4.9 and 6.0 percent, respectively.

Attention may here be drawn to the fact that, insofar as the culling of the less productive sows had an effect on the variability among the litters produced by older sows, one would not expect the apparent effect of age of dam to be the same had no culling been practiced. No method was found to determine the importance of the influence of culling when based on the various factors that were taken into consideration in replacements of breeding stock. However, by an analysis of multiple covariance involving litter size as the dependent variable and the inbreeding of the sows as an independent variable it is possible to show whether differences in the inbreeding of the sows contributed to the effect of culling. When such an analysis was made, age of dam still was found to account for almost as much of the variance as that calculated before allowance was made for inbreeding. It is probable, therefore, that most if not all of the culling was based on factors other than those attributable to differences in inbreeding.

Influence of Sire

To determine whether there was any difference among litters sired by different boars, all litters having the same sire and farrowed in the same year were grouped together. When this procedure was followed and when correction was made for the inbreeding of the litters

and sows by a multiple covariance analysis, differences between sires were found to be nonsignificant for number of pigs per litter at birth. In litter size at 28 days and at 70 days of age, on the other hand intrayear differences between sires proved to be highly significant and accounted for 11.9 and 10.5 percent, respectively, of the total variance in the number of pigs per litter at those ages.

The results for litter size at birth are in close agreement with the findings of Haring (*3*), Johansson (*4*), Wentworth (*11*), and others, and give added support to the view that the sire has no direct influence on the number of pigs a sow farrows. The conclusion indicated by the results for litter size at 28 days and at 70 days of age, on the other hand, is that there was a higher mortality among the pigs sired by some boars than among those sired by others. It is conceivable, of course, that differences in the genetic make-up of pigs sired by different boars were at least partly responsible for the differences in mortality of their offspring, but since the matings were not strictly at random there is good reason to believe that conditions peculiar to the nursing and mothering ability of the sows to which each sire was mated were a more important cause of the differences in the viability of the pigs when grouped according to sires.

Influence of Dam

The variance between litters from the same sow, when compared with that between all litters considered as a single population, indicates that conditions peculiar to individual sows account for 20.2 percent of the variance in litter size at birth, for 19.6 percent in litter size at 28 days, and for 21.3 percent in litter size at 70 days of age. These figures show that among the sows of this herd the average correlations between litters from the same sow were 0.20 for number of pigs farrowed, 0.20 for litter size at 28 days, and 0.21 for litter size at 70 days.

If heredity were the only cause of the individual differences between sows, the hereditary part of the variance would amount to about 20 percent of the total variance in litter size at each age. Since other factors, such as differences in health or nursing ability peculiar to individual sows, undoubtedly were partly responsible for those differences, it is probable that less than 20 percent of the variance was really hereditary.

So far as there was a tendency for inbreeding to result in the segregation of lines differing in litter size, the hereditary portion of the variance is larger than it would have been in a herd not subjected to inbreeding. When correction was made for the inbreeding of sires and litters by an analysis of multiple covariance, the average correlations between litters from the same sow were 0.13 for number of pigs farrowed, 0.16 for litter size at 28 days, and 0.20 for litter size at 70 days of age. These correlations are somewhat lower than those previously given, indicating that the inbreeding practiced probably increased the portion of the variance attributable to genetic differences between sows. Similar correlations were reported by Lush and Molln (*8*) for litter size at birth and at weaning.

DISCUSSION

The results of this study show that only a relatively small part of the variance in litter size is hereditary in character. This conclusion is based on the fact that the genetic part of the variance was found to account for not more than 20 percent of the variance in litter size at birth, at 28 days, or at 70 days of age. Although this figure seems too small to indicate that selection would bring about rapid improvement in this character, it supports the conclusion that the gradual decline in litter size over the 17-year period was at least partly genetic.

As regards the relative importance of other factors affecting litter size, it would seem that uncontrolled environmental conditions, such as temporary changes in health of the sows or in their fertility, are a much more important cause of variation in litter size than such factors as yearly changes in feeding and management, season of birth, and age of sows at farrowing. Even if allowance were made for all these latter causes, which at best account for 20 percent of the variance, approximately 60 percent of the variance in litter size at each age remains as attributable to causes the nature of which is not clear.

These results, although of limited practical value, furnish an adequate explanation of the many disappointments experienced by breeders in attempting to improve such a character as litter size. But in spite of this, the genetic portion of the variance seems large enough to suggest that selection may bring about changes in this character. That such changes have been accomplished is indicated by the fact that material breed and strain differences in litter size occur and that, as shown in this experiment, this character is influenced by inbreeding.

SUMMARY

The records of 362 litters of Chester White swine farrowed over a 17-year period were analyzed to study the effects of inbreeding on the number of pigs per litter at birth, at 28 days, and at 70 days of age, and to evaluate the importance of other causes affecting this character at each of these ages.

As a consequence of inbreeding the general trend of litter size at birth, as well as at 28 days and at 70 days, was downward. Differences in the inbreeding of the litters appear to have had a greater effect on litter size at the various ages than did differences in the inbreeding of their sires and dams.

Yearly differences in feeding and management apparently had no significant influence on number of pigs at birth, but there was a significant effect of this factor at 28 days and 70 days of age. Spring-farrowed litters were slightly larger than fall-farrowed litters, but the difference was significant only for litter size at 70 days of age.

There was a tendency for litter size to increase with an increase in age of dam to about 3½ years, after which it remained practically unchanged to the age of 5½ years. Age of dam accounted for about 10.7 percent of the variance in number of pigs per litter at birth, for 4.9 percent in the case of litter size at 28 days, and for 6.0 percent in the case of number of pigs weaned.

Differences in the individuality of the sires had no direct influence on number of pigs farrowed. However, there was a significant difference in number of pigs at 28 days and at 70 days of age.

Less than 20 percent of the variance in litter size at any one of the three ages was found to be hereditary in character. Season of birth, yearly changes in feeding and management, and differences in age of dam appeared to account for another 20 percent of the variance. The remainder, or about 60 percent of the variance, was due to causes the nature of which could not be determined.

The general results of this study indicate that in spite of the relatively large proportion of the variance in litter size outside the breeder's control, he should be able to exert a favorable influence on this characteristic through a program based on selective breeding and closely supervised management.

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